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Olfactory *and* tactile cues can guide near-distance location of a refuge by whip spiders (Arachnida, Amblypygi)

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Whip spiders (Order Amblypygi) are arachnids with greatly elongated, antenniform first legs that serve a sensory rather than locomotory function (Weygoldt, 2000). In their natural habitat, whip spiders faithfully occupy home refuges, and if experimentally displaced from them, can navigate back (Beck & Görke, 1974; Hebets, Gering, Bingman, & Wiegmann, 2014). If the tips of the antenniform legs (which bear olfactory sensilla) are clipped off or coated in nail polish, experimentally displaced whip spiders fail to return to their refuges (Beck & Görke, 1974; Bingman, Graving, Hebets, & Wiegmann, 2017; Hebets, Aceves-Aparicio, et al., 2014). Thus, it has been proposed that olfactory cues guide the homing behaviour of whip spiders (Beck & Görke, 1974; Bingman et al., 2017; Hebets, Aceves-Aparicio, et al., 2014; Wiegmann et al., 2019). An element of this olfactory hypothesis has now been explicitly tested by Wiegmann et al. (2019), which demonstrates the ability of whip spiders to learn and use olfactory cues to locate a refuge in the laboratory, and that this ability is disrupted after the tips of the antenniform legs are clipped.

In pursuit of this olfactory hypothesis the fact that whip spiders can also use tactile cues to locate a home refuge in the laboratory (Santer & Hebets, 2009), and the possibility that these cues might be important in the natural habitat, has been neglected. The tips of a whip spider's antenniform legs are equipped with a range of sensillum types, including but not limited to, olfactory, contact chemosensory, and mechanosensory hairs (Igelmund, 1987; Santer & Hebets, 2011). In field experiments, clipping off the *ca.* 20 distal segments at the tips of the antenniform legs has been interpreted as a primarily olfactory manipulation because it removes all olfactory sensilla whilst leaving some of the other types present elsewhere (Bingman et al., 2017; Hebets, Aceves-Aparicio, et al., 2014). Although the possibility of disruption to sensation in other modalities has been acknowledged (Hebets, Aceves-Aparicio, et al., 2014), this interpretation overlooks the special importance of tactile sensory structures at the antenniform leg tips. The antenniform legs of whip spiders are equipped with an array of at least seven giant sensory afferents with cell bodies located within the distal segments of the antenniform leg (Igelmund & Wendler, 1991a, 1991b; Santer & Hebets, 2011; Spence & Hebets, 2006). Four of these giant neurons (GNs) have characterised

mechanosensory functions and receive inputs from known fields of mechanosensory sensilla at the antenniform leg tip. GN1 and GN2 each receive inputs from bristle sensilla in two overlapping fields that each includes some of the most distal 20 segments of the antenniform leg (Igelmund & Wendler, 1991a, 1991b; Spence & Hebets, 2006). GN6 and GN7 are excited via a slit sensillum responding to movement at the articulation between the 21st and 22nd segments of the antenniform leg tip (Igelmund & Wendler, 1991a; Spence & Hebets, 2006). Furthermore, high-speed cinematography reveals that when examining surfaces, whip spiders tap, press, and scrape the tips of their antenniform legs against the surface in a way that might allow the spike trains of these four giant neurons to encode tactile information like shape and texture (Santer & Hebets, 2009, 2011). There can be no doubt that clipping off or covering *ca.* 20 distal segments at the tips of the antenniform legs would disrupt tactile sensory input to these giant neurons, and the former manipulation might damage or destroy the giant neurons themselves. Thus, the disruption of tactile sensation might also contribute to the inability of whip spiders to locate their home refuge after such an experimental manipulation. Most importantly, laboratory experiments *have already shown* that whip spiders have the ability to learn texture cues and associate them with a refuge (Santer & Hebets, 2009).

The motivation of this note is not to refute the findings of Wiegmann et al. (2019): that work demonstrates that olfactory cues can be used by whip spiders to locate a refuge, and that clipping off the tips of the antenniform legs disrupts that ability. However, this note does emphasise that there is also physiological and behavioural evidence supporting the use of tactile cues in such near-distance location of a refuge. In another extraordinary animal navigator, the desert ant *Cataglyphis*, experiments show that visual (Collett, Dillmann, Giger, & Wehner, 1992), olfactory (Steck, Hansson, & Knaden, 2009), and tactile cues (Seidl & Wehner, 2006), can all contribute to the accurate location of the nest. Wiegmann and colleagues anticipate that whip spider navigation also relies on multimodal sensory cues (Wiegmann, Hebets, Gronenberg, Graving, & Bingman, 2016), and in that multimodal context the tactile sensing abilities of these fascinating animals should not be overlooked (c.f. Santer & Hebets, 2009).

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